SPONGIOPHYTON FROM THE LATE LOWER DEVONIAN OF NEW BRUNSWICK AND QUEBEC, CANADA

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ABSTRACT. Compressed cuticles of the dorsiventral, presumed parenchymatous land plant *Spongiophyton* are described from several late Lower Devonian (Emsian) localities in northern New Brunswick and Gaspé, Quebec. They are assigned to *Spongiophyton minutissimum* Kräusel. Thalli branch dichotomously several times in more than one plane and also produce short vertical branches. No reproductive structures are present. The cuticle is thicker dorsally, often being up to 250 μm thick as opposed to 30–60 μm for the ventral cuticle. Small circular to elliptical pores occur on the dorsal surface or along thallus margins. The many specimens obtained provide considerable information on variation in vegetative morphology and suggest a growth habit similar to some extant thallose liverworts. This new information expands the concept of *S. minutissimum* and supports the genus as a taxon quite distinct from *Nematothallus*, *Prototaxites*, or other plants with a putative filamentous organization. Absence of reproductive structures precludes improved understanding of *Spongiophyton's* relationship to algae or vascular plants; the presence of a resistant cuticle argues against these plants representing algae. They may instead represent a transitional grade between algae and higher plants. The new specimens also demonstrate that these cuticles are susceptible to some differential breakdown as a result of oxidation or heat. Degradation features include superficial cracks or pockmarks, a spongy appearance, or a pseudocellular pattern. It is suggested that possibly some features of other enigmatic Devonian plants (e.g. *Orestovia*, *Rhytidophyton*, etc.) may have resulted from degradation of their very thick cuticles.

IN addition to the many genera of vascular plants that are known to occur in the Lower Devonian of New Brunswick and Gaspé (for a summary see Gensel 1982), a variety of non-vascular plant types also are present. These may represent several genera and most probably several different lineages of non-vascular plants, many of which still require detailed study. This paper describes one very abundant form, obtained from several outcrops of Early Devonian rocks in New Brunswick and Gaspé, Quebec, referable to *Spongiophyton minutissimum* Kräusel.

These fossils were first collected by Sir J. W. Dawson and briefly described in his introductory comments appended to Penhallow's publication on *Prototaxites* of 1889. In those comments, Dawson (p. 34) noted 'In the sandstones of Gaspé basin there occur laminae of a resinous substance resembling amber …' which often were associated with carbonaceous films. He concluded that these entities represented a secretion of the bark of some tree, suggesting somewhat indirectly that the source may have been *Prototaxites*.

Our investigations show that these fossils are not resinous secretions but rather are cuticles of thalloid organization referable to *Spongiophyton*, first described from the Middle Devonian of Brazil by Kräusel (1954). Kräusel established the family Spongiophytaceae to include *Spongiophyton*; this family subsequently was expanded to include up to 6 genera (listed in Table 1). Despite the diverse array of thalloid organisms included in the Spongiophytaceae, definitive evidence on their more exact affinities does not exist. They have been regarded as enigmatic terrestrial thallophytes with no known modern counterparts, possibly related to an algal division. All possess one feature not yet found among algae, namely a resistant cuticle. Whether or not all of the genera included in this family are closely related to one another remains uncertain.

Sommer (1959) recorded the genus in several Lower Devonian localities in the Brazilian states of Parana, Boias, Piaui, and Maranhao and in western Bolivia. Kräusel and Venkatachala (1966)

TABLE 1. The six genera attributed to the Spongiophytaceae, with number of species in each and their distribution.

Genera	No. of species	Geographic distribution
Spongiophyton Kräusel	4	Brazil, Ghana, Canada, Poland(?), Bolivia(?)
Aculeophyton Kräusel and Venkatachala	2	USSR (Siberia), Brazil
Orestovia Ergolskaya	5	USSR (Siberia, Voronezh and other regions), China
Orestovites Istchenko and Istchenko	1	USSR (Voronezh region)
Rhytidophyton Istchenko and Istchenko	2	USSR (Voronezh region)
Voronejiphyton Istchenko and Istchenko	1	USSR (Voronezh region)

provided comparative data on several species of *Spongiophyton*, and suggested that *S. hirsutum* possibly belonged to their newly described genus *Aculeophyton*. They also described fossils as *Orestovia* from the Lower Devonian of Yunnan Province, China. They placed both *Aculeophyton* and *Orestovia* with *Spongiophyton* in the family Spongiophytaceae. Zdebska (1978) described fragments from a borehole in Poland as *Spongiophyton*, but Edwards (1982) suggested that these remains, particularly Zdebska's species 2, may have more features in common with cuticles attributed to the nematophytes than *Spongiophyton*. Chaloner *et al.* (1974) provided a detailed description of specimens from the Middle Devonian of Ghana which expands the circumscription of *Spongiophyton nanum* and documents the occurrence of remains similar to *S. lenticulare*. Boureau and Pons (1973) described remains from southern Bolivia which they assigned to *Spongiophyton lenticulare*, using these and associated plant remains to date the sediments as Early Devonian. Their identification may need reconsideration. Our report represents the first undoubted record of *Spongiophyton* from the Early Devonian.

Several similar types of plant, some of them included in the family Spongiophytaceae, were described by Istchenko and Istchenko (1981), thus demonstrating the existence of spongiophytes *sensu lato* in the Middle Devonian in parts of Russia. Some of these exhibit similar morphology to *Spongiophyton*, while others differ in cell construction. Again, their exact relationships are not clear.

The rather widely-ranging geographical distribution of the Spongiophytaceae *sensu lato*, including the fossils discussed here, is summarized in Table 1. The genus *Spongiophyton* occurs, without doubt, in South America and Africa at a high palaeolatitude (60° S or greater) in the Devonian. This report documents its presence in Laurussia-associated microcontinental plates at approximately 20–30° S. This might suggest that the plant exhibited a broad temperature tolerance, since the southern Gondwanan continents contain faunas indicating cool temperatures at that time (see Boucot 1985; Livermore *et al.* 1985; Scotese *et al.* 1985). Other genera attributed to the family Spongiophytaceae occur between 0° and 30° N palaeolatitude in Laurussia (?), Kazakhstania, Siberia, and China, where some form coals.

The abundance of *Spongiophyton* in the Canadian localities suggests that it was a common element of the vegetation, forming large populations in some areas. The large numbers of individual thalli obtained at some localities provide new information on the overall organization of the cuticularized thallus and on aspects of variation in this genus.

TEXT-FIG. 1. The occurrence of *Spongiophyton minutissimum* (heavy-type S) at various localities in New Brunswick and Quebec, showing their range in terms of the spore assemblage zones. Specific localities are discussed in the text.

Series	Stage	Provisional Spore Assemblage Zones and Subzones (McGregor, 1973, 1977)	Outcrops along Restigouche River, New Brunswick[1]	Outcrops along north and south shore of Gaspé Bay, Quebec[2]
Middle Devonian	Eifelian			
Lower Devonian	Late Emsian	annulatus-lindlarensis / Grandispora	B H,I H - S A,E F K - S L	X V,W
	Early Emsian	sextantii / caperatus emsiensis	P - S Q - S M - S N - S	S,T - S U - S Y - S
	Siegenian			

([1] Outcrops designated A - N.)

([2] Outcrops designated S - Y.)

TEXT-FIG. 1. For legend see opposite.

LOCALITY AND GEOLOGY

The major localities yielding *Spongiophyton* are listed below and in Text-figure 1; these include some of Dawson's localities as well as other outcrops in New Brunswick and Gaspé, all of late Lower Devonian (Emsian) age.

1. Atholville, New Brunswick: Route 17 roadcut into Atholville (Locality P, Text-fig. 1) and outcrop along Beauvista Drive (Locality Q, Text-fig. 1). Specimens occur scattered on bedding surfaces of channel fills at the former and as stacks of individuals in grey bands of poorly-bedded sandy claystone at the latter.

2. Localities H, K, M, and N (Gensel and Andrews 1984; Text-fig. 1) along the Restigouche River, near Dalhousie Junction, New Brunswick, from which several vascular plants have been described (Gensel 1982). The thalli are sporadic and usually are intermixed with the more abundant vascular plant remains.

3. Cross Point, Quebec: at the Bordeaux Quarry and just to the north along Route 132. These rocks were included in the Gaspé Sandstone Group (McGerrigle 1950; Alcock 1935) and may fall within the LaGarde Formation of Dineley and Williams (1968). The Bordeaux Quarry, one of Dawson's collecting sites, consists of a sequence of red-brown sandstones alternating with conglomerate bands. The thalli occur in the sandstone along with slender ribbed axis (?*Psilophyton*) and *Prototaxites* 'logs'. These same sediments are exposed along a new roadcut on Route 132, where bedding surfaces show alternating conglomerate and sandstone layers, with the latter being a thin 'wash' of pebbles. Thalli densely cover the bedding surfaces of the sandy layers; a specimen of *Prototaxites* about 5 m long and 0·8 m wide and numerous smaller ones also were found in or immediately adjacent to these layers.

4. At several horizons of the Battery Point Formation near Cap-aux-Os, Gaspé and along the Laurencelle road which leads from Cap-aux-Os to Cap-des-Rosiers Est, Gaspé Peninsula, Quebec (localities S, T, U, Y of Gensel and Andrews 1984; Text-fig. 1). Thalli are rare to fairly abundant and appear to have been transported.

5. South shore of Gaspé Bay at several localities. (See McGregor 1977 for stratigraphic correlations.)

TAPHONOMY, MATERIAL AND METHODS

Considerable variation in mode of burial exists among thalli obtained from these outcrops. The majority are spread along bedding planes of fluvial, often channel-deposited sediments, with no preferred orientation (Pl. 1, figs 1 and 5), suggesting they were transported moderate distances prior to deposition. At locality Q, thalli occur in stacks several entities deep and are so tightly held together that it is difficult to determine if they represent one plant or several (Pl. 1, figs 2–4). Thick coverage of some bedding surfaces by many such stacks suggest that these thalli were growing in considerable abundance in some areas and buried rapidly near (or at?) their site of growth. We tend to discount the possibility that the stacks of thalli resulted entirely from the way in which they grew because they are not all orientated the same way up within a stack.

The thalloid plants are preserved as compressed cuticles which occasionally show impressions of internal cells, thus mostly demonstrating general morphology. We use the term *cuticle* to refer to the inert outer covering of these fossils. It is resistant to oxidative maceration and shows a pattern of cell outlines on the inner surface, features found in the cuticle of higher plants. Its chemical composition is unknown, but its morphology compares closely with the lipid-derived cuticle known to occur only in embryophytes (higher plants). Although some algae apparently possess a thin, protein-rich outer covering that withstands some acid hydrolysis (Hanic and Cragie 1969), these have not been shown to be resistant to coalification during fossilization.

EXPLANATION OF PLATE 1

Figs 1–7. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. 1–5, various ways the thalli occur in the sediment; 1, specimen from Route 132, Quebec locality with numerous scattered thalli on the bedding plane; this specimen was etched in HF, GSC 93004, × 0·8. 2, surface view of mass of thalli from a poorly bedded siltstone, Atholville locality, New Brunswick, GSC 93003, × 1·2. 3, lateral view of mass of stacked thalli, Atholville locality, New Brunswick, GSC 93005, × 1·4. 4, mass of stacked thalli from Atholville; N.B. locality, isolated by maceration in HF, GSC 93008, × 3. 5, numerous thalli after etching a single bedding plane, locality N, New Brunswick, GSC 93006, × 1·2. 6, SEM of thallus isolated by maceration, distal region to left; basalmost divisions produce upper and lower lobes (a), next 1–3 divisions produce side-by-side ones (b); note constrictions in lobes, pores (some indicated by arrows); roughness and cracks probably produced by deterioration under SEM vacuum, × 10. 7, thallus fragment with four dichotomies mostly in same plane, some with apices preserved, poral surface up, lying on etched surface of sediment, GSC 93011, × 4.

PLATE I

GENSEL, CHALONER and FORBES, *Spongiophyton*
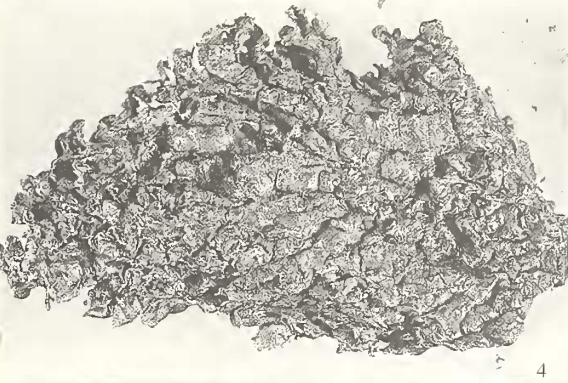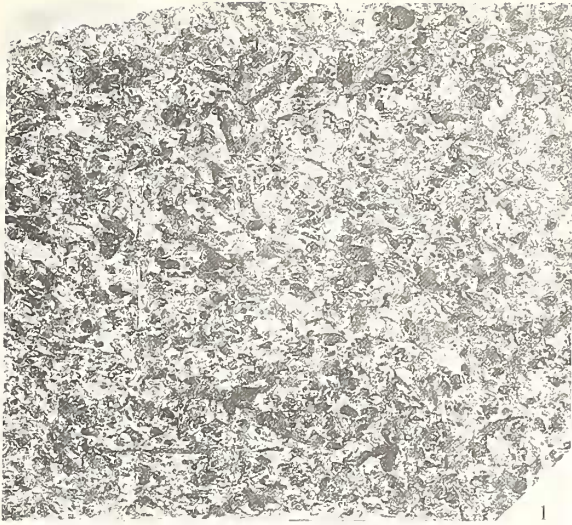
The cuticles range from a shiny to dull black or brown colour to ones which are naturally weathered to a red-brown colour. Some lighter coloured portions, especially distal tips, appear waxy. A single specimen may exhibit some portions that are red-brown and others, black; possibly it was specimens of this kind which caught Dawson's eye. Thallus surfaces range from smooth to finely pockmarked to rough in texture; the latter may have been partially corroded during diagenesis. At the Rte. 132, Quebec locality, the sandstone matrix apparently has imprinted outlines of grains on the thalli, causing a distinctive deeply pockmarked surface pattern.

Individual thalli, or regions of a given thallus, vary in the extent to which the cuticle is eroded. Many splits and cracks are present, and more may be induced during SEM treatment. Features we interpret as resulting from erosion include differences in pore outline, the frequent absence of the thinner, here designated lower, part of the thallus, and the depressions located at branch tips.

Bulk maceration of specimens in HF provided best results in elucidating thallus morphology. Thalli cleared only after long oxidation in Schulze's solution. Individual fragments reacted slightly differently to oxidation, suggesting that alteration of the original substance prior to or during fossilization was quite variable. Selected specimens were cleared in Shulze's solution at timed intervals, being examined and photographed with a light microscope at 10, 30, and 60 minute intervals. At the end of 48 hours, no evident destruction of surface features, or changes in pore outline or size, were observed in well-preserved specimens. In poorly preserved thalli (partially oxidized, possibly more strongly compressed), pores became progressively more irregular in outline with prolonged maceration. Extensively cleared thalli may appear 'cellular' as a result of differential breakdown of the thick cuticle (Pl. 3, figs 5 and 6). Differential erosion, particularly of the inner cuticle surface, is evident in thin sections (Pl. 3, fig. 1). After long maceration the cuticles appear spongy in construction (Pl. 3, fig. 7). This probably was the basis for Kräusel's original suggestion of a spongy structure (Schwammstructur) of the thallus (see also Chaloner *et al.* 1974, p. 934).

To determine regularity of pore spacing, camera lucida drawings were made of specified areas of selected specimens. Using a customized software program called MEASUR (S. Case, pers. comm.) pore location was digitized, spacing calculated, and mean nearest neighbour determined. No regular pattern was evident.

Rock fragments containing numerous thalli and individual thalli isolated by maceration in HF were embedded in plastic, sectioned, and ground thin until transparent. Isolated thalli also were embedded in araldite or glycol methacrylate, sectioned with a microtome, and examined with LM and TEM for ultrastructural detail.

Both oxidized and unoxidized specimens were mounted on slides in CMC non-resinous mounting medium, or were glued to glass or cardboard slides with gum tragacanth. Isolated thalli were also mounted on stubs, coated with gold-palladium and examined with an ETEC SEM. Specimens were photographed using a Leitz Aristophot, a Wild Photomacroscope, or a Zeiss photomicroscope. Type and figured specimens are stored in the collections of the Geological Survey of Canada at Ottawa, Ontario and bear the numbers GSC no. 93003–93020.

SYSTEMATIC PALAEONTOLOGY

Family SPONGIOPHYTACEAE Kräusel, 1954
### Genus SPONGIOPHYTON Kräusel, 1954

Type species. Spongiophyton lenticulare (Barbosa) Kräusel, 1954, p. 206, figs 5–7 of Barbosa, 1949; from the upper Punta Grossa beds, Parana, Brazil.
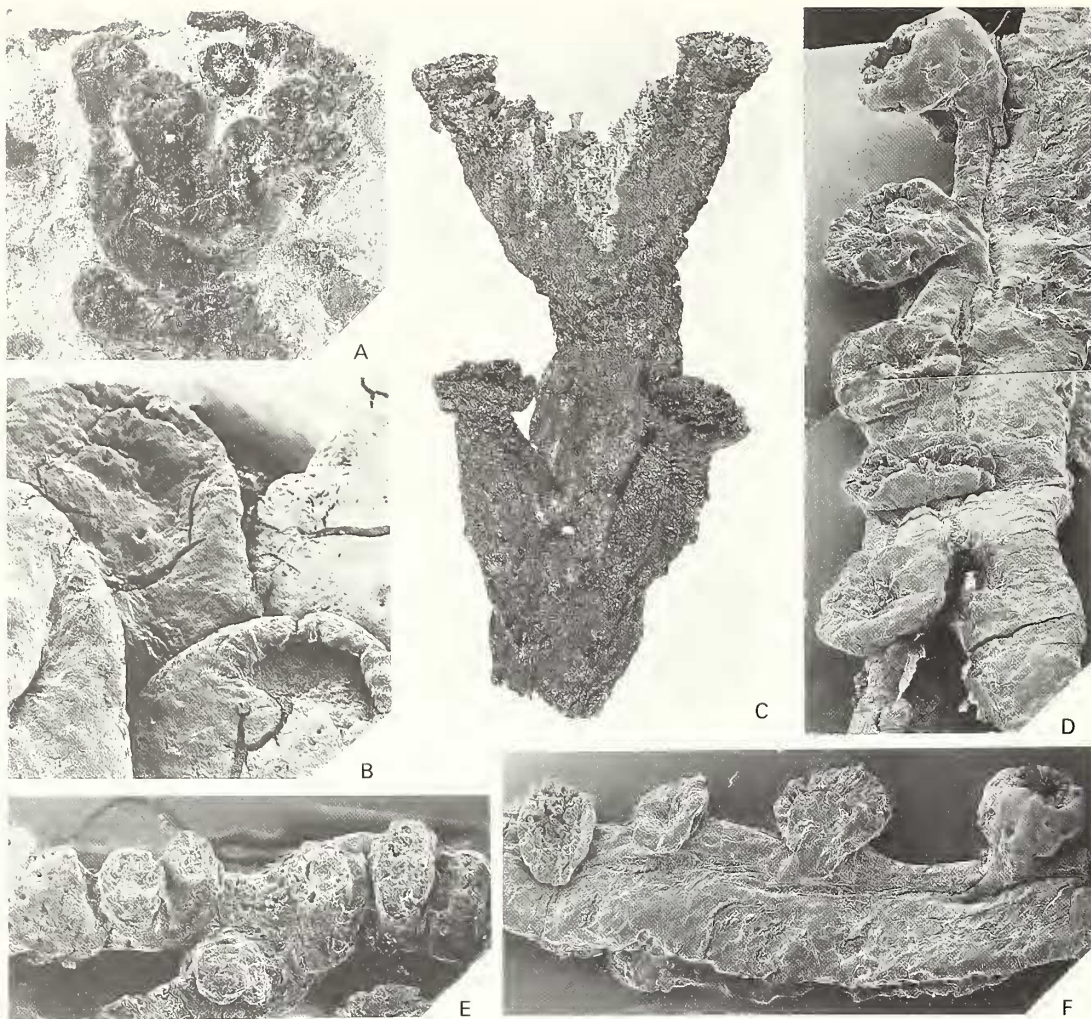
S. minutissimum Kräusel, 1954

Plates 1–3; Text-figs 2–6

Type specimens. P. 264/9, Kräusel (1954), Pl. 28, figs 72 and 73.

Original diagnosis. Thallus klein, meist nur wenige mm messend, gabelig gelappt, mit stark verdickten Rädern. Innenbau wie bei *Sp. nanum*, die zahlreichen Löcher aber klein, nadelstichartig, ihre Durchmesser meist 60 bis 100, selten bis 150 μm, oft quer verbreitert, Oberflächenzellen wabig-vieleckig.
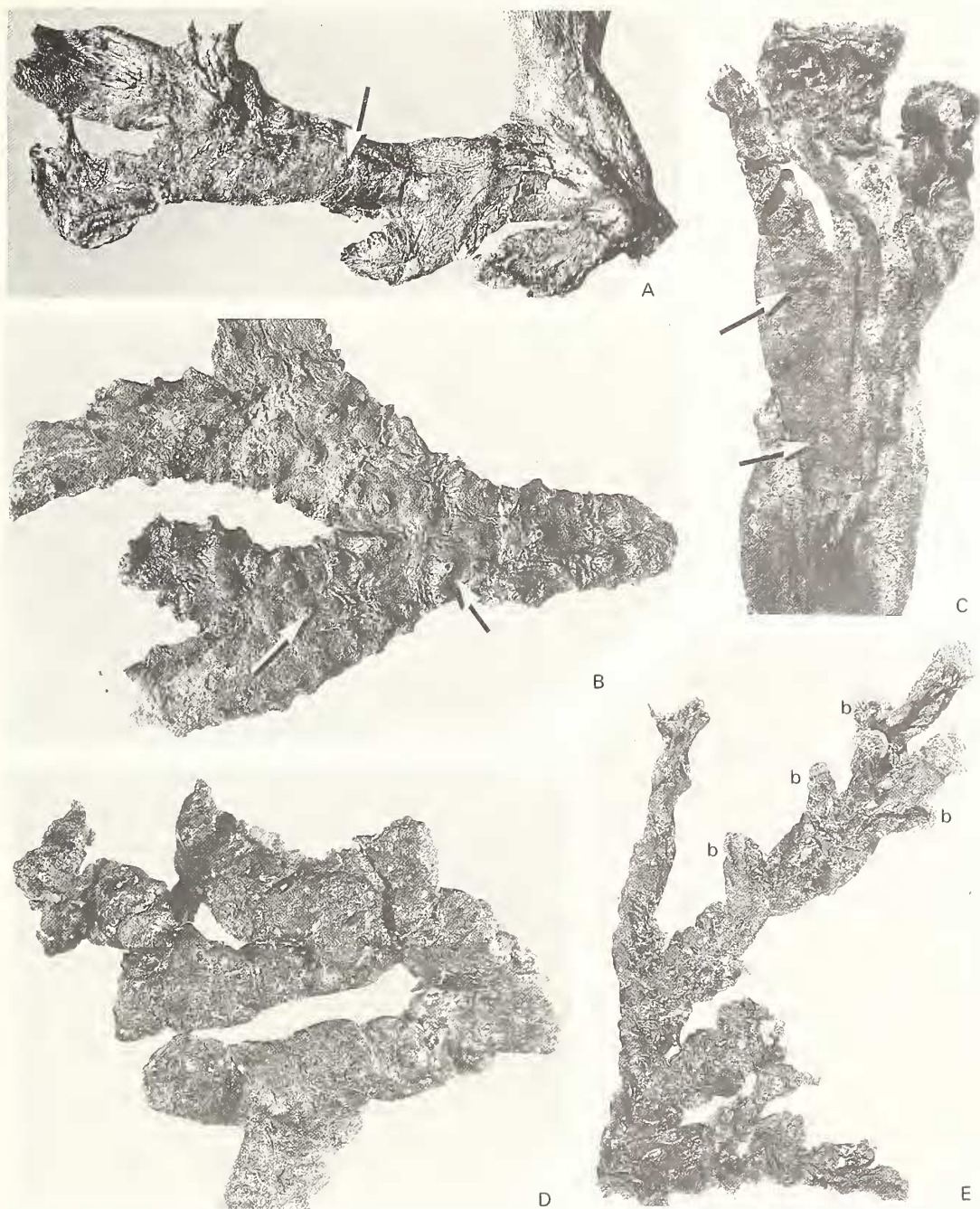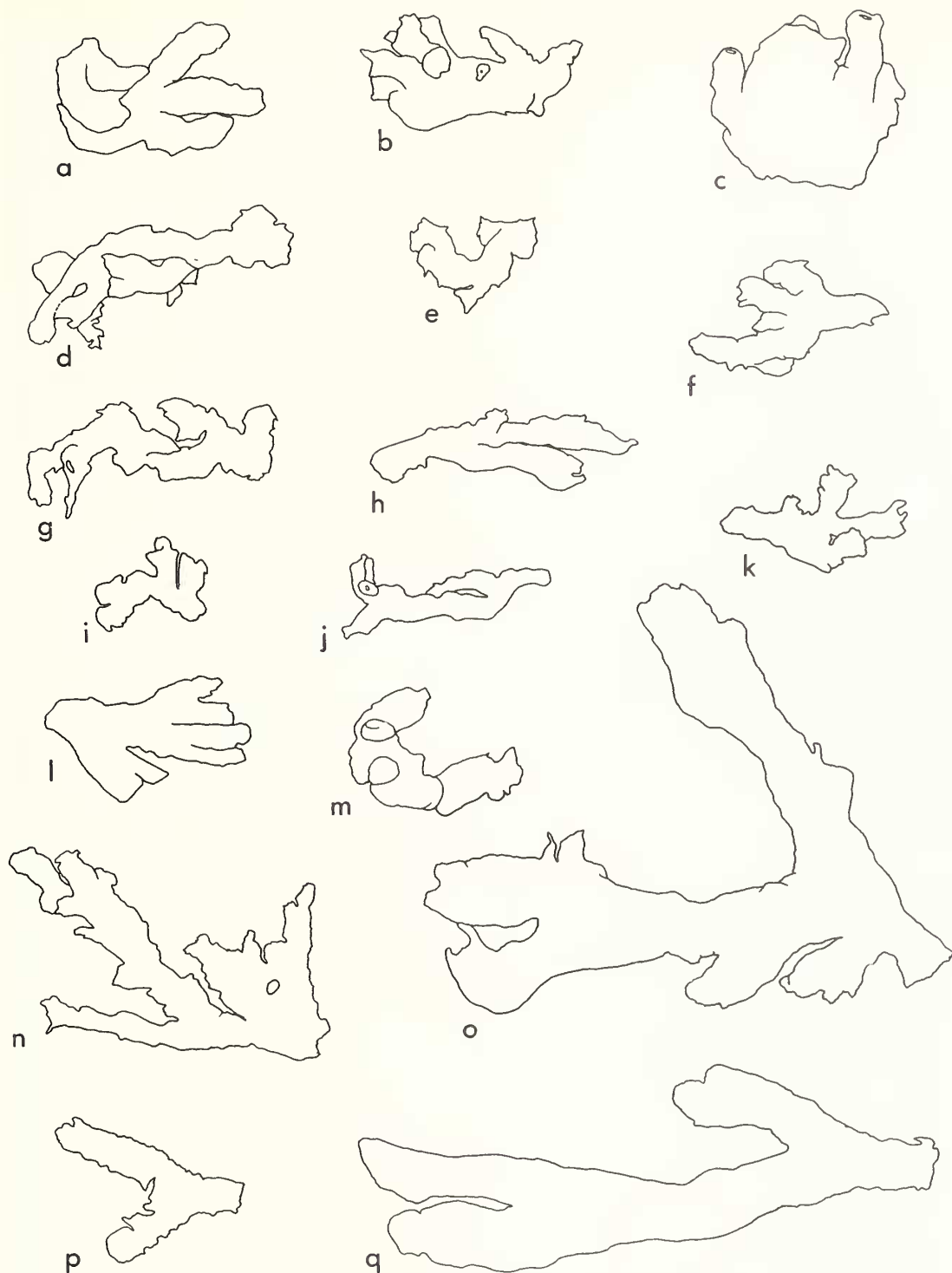
TEXT-FIG. 2. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. A, form 3 thallus, poral side up, with smooth to finely ridged surface and few pores (one at arrow); branching is mostly in one plane; wrinkling and constrictions near lobe apices are interpreted as a result of preservational factors, GSC 93012, × 7. B, form 2 thallus, poral surface up, with many pores (arrows), each pore located in raised area of surface producing bumpy appearance. GSC 93013, × 12. C, form 3 thallus fragment isolated by maceration, showing two dichotomies in two different planes, but with lobes parallel (arrows indicate pores), GSC 93010, × 14. D, form 1 thallus with numerous constrictions, dichotomies in same plane, numerous pores, GSC 93015, × 12. E, form 1 thallus bearing numerous short branches (b) as well as exhibiting major dichotomies, GSC 93016, × 9.

TEXT-FIG. 3. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. A, an isolated thallus with several lobe apices visible, after short HF etch; from sequence near *Sawdonia acanthotheca* locality (locality M), New Brunswick, GSC 93007, ×6. B, SEM of horizontal thallus lobes; note breakdown of apex to right and absence of spores or other cell masses in depression, ×46. C, LM of thallus with two pairs of lobes, intermediate between short vertical branches and 'normal' lobes, departing from poral surface; lobe apices collapsed, GSC 93017, ×10. D and F, SEM of thalli with short vertical branches departing from poral surface; apical depressions are probably a result of collapse of thinner cuticle in that area; D, ×15; F, ×11. E, SEM of thallus with very pronounced constrictions and possible short vertical branches near left, pores, ×12.

Emended diagnosis. Thallus cylindrical, originally circular or elliptical in cross section and at least 2 cm long. Width of thalli 0·2–5·5 mm. Thalli may exhibit constrictions along their length. Thalli branch dichotomously several times, with most lobes 3–10 mm long and with rounded apices. Short erect branches (1–2 mm long) occur on poral surface of some thalli. Pores extend through cuticle mostly on one surface, this being 2–4 times thicker than aporal surface (75–250 μm *vs* 30–60 μm), the thicker cuticle extending around the margins onto the edge of the aporal surface. Poral and aporal surfaces smooth, aporal surface often longitudinally folded. Inner surfaces of cuticle may

TEXT-FIG. 4a–q. Camera lucida drawings of various *Spongiophyton minutissimum* thalli, showing differences in extent and angle of branching, ×6.

retain rectangular cell outlines, 20–43 μm long and 9–12 μm wide, although often degraded and vermiform in appearance. Pores circular to oval, randomly spaced, 22·5 × 9 μm to 99 × 90 μm in diameter, with vertical, fissured or (occasionally) bevelled edges.

Description. The plant fossils consist of the very thick cuticles of dorsiventral, apparently elliptical thalli which dichotomize at various intervals and on the surface of which pores occur (Pl. 1, figs 6 and 7; Text-figs 2–4). Thalli vary mainly in size, pore density and location, extent of branching, and surface features. Three categories (forms 1–3) of thalli are recognized: (1) the majority are smooth-surfaced, with a number of pores located on the upper surface, many branches, and 'constrictions' (Pl. 1, figs 6 and 7; Text-fig. 2D, E); (2) some are smooth-surfaced except that each pore occurs in a small projection resulting in an overall bumpy appearance (Text-fig. 2B); and (3) some thalli are smooth but longitudinally ridged, have very few pores located along lateral margins, and bear short vertical branches (Text-figs 2A, C and 3C). We presently regard this variability in surface topography, pore distribution, and branching type to be intra-specific, perhaps resulting from different parts of a given plant being represented, populational differences, and/or preservational differences. We thus refer all of the specimens to a single species.

The dorsiventral thalli are usually incompletely preserved, being up to 10 mm long and ranging from 0·3–2·5 mm wide (Pl. 1; Text-figs 2 and 3). The thick amorphous cuticle is smooth externally (Text-figs 2 and 3) and rough internally (Text-fig. 5C, D). One surface of the cuticle is thicker than the other (Pl. 3, figs 1 and 3); we interpret the thicker surface, on which pores and branches occur, to be the dorsal surface of a more or less flattened horizontal thallus. Pores may also occur near the margins on both upper and lower surfaces of some (especially form 3) thalli.

The thalli branch dichotomously at least six times at 0·2–3 mm intervals, being dense on some specimens and very sparse on others. Branching results in formation of lobes extending in the same plane as the original thallus (Pl. 1, fig. 7; Text-figs 2A, B and 3C) or in lobes lying one on top of the other but still with their long axes parallel (Pl. 1, fig. 6; Text-fig. 2C). These may curve upwards, downwards or laterally (in relation to the presumed horizontal position of the main thallus). It is not unusual to observe three to four levels of thallus lobes belonging to one specimen in the stacks of fossils preserved at the Atholville locality. Additionally, branching may result in one horizontal and one short vertical lobe at right angles to each other (Text-figs 2E and 3D, F).

Constrictions occur within the lobes of some thalli resulting in a sausage-string type of appearance (Pl. 1, fig. 6; Text-figs 2D, E and 3E. The region between some constrictions almost resembles very short upright branches.

The upright branches are 1–2 mm tall and occur singly or in 2 rows (Text-fig. 3D, F). While upright branches occur on all forms of thalli, they are most abundant on form 3, being located along a central ridge area. Most exhibit pores (Pl. 2, fig. 2). The branches are narrower towards their base and swell or flare distally (Text-fig. 3A, C, D, F). Some of these branches terminate in rounded apices, often with a slight depression (Pl. 2, fig. 1; Text-fig. 3A). A few exhibit small protrusions extending from the apex (Pl. 2, figs 3 and 4) while others have at their tips a deep cup-like depression which usually is irregular in outline (Pl. 2, fig. 2). The interior of the cup revealed no organization such as spores or vegetative propagules. Their structure suggests the depressions formed as a result of collapse and breakdown of cuticle at the branch apex. Horizontal branch tips exhibit similar depressions (Text-fig. 3B).

Circular to oval shaped pores occur on the presumed upper (and thicker) surface of the first two forms of thalli and along the margins of the third form of thallus (Pl. 1, fig. 6; Pl. 3, figs 5 and 6; Text-fig. 2B–D). They are variably spaced, from 3·5 μm to 350 μm apart. Average distance between pores on selected specimens are 30, 53, 75, 178, 222 μm. The pores range in size from 22·5 μm long by 9 μm wide to 99 μm long by 90 μm wide. SEM study shows the pore margin often to consist of indented fissures or rounded outlines (Pl. 2, figs 4 and 6; Text-fig. 5B). Only a few exhibit a bevelled edge (Pl. 2, fig. 5) as has been described in *Spongiophyton nanum* by Chaloner *et al.* (1974).

EXPLANATION OF PLATE 2

Figs 1–5. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. 1 and 2, SEM of apical region of vertical branches showing various degrees of collapse; 1, × 40; 2, × 31. 3 and 4, general view and detail of short vertical branches with protrusion at apex – also appearing somewhat degraded; note occurrence of pores on branches (arrows); 3, × 38; 4, × 120. 5, SEM of pore with bevelled edges, some evidence of internal surface of cuticle, × 1100. 6, SEM of pore with irregular margin, × 120.

PLATE 2

GENSEL, CHALONER and FORBES, *Spongiophyton*
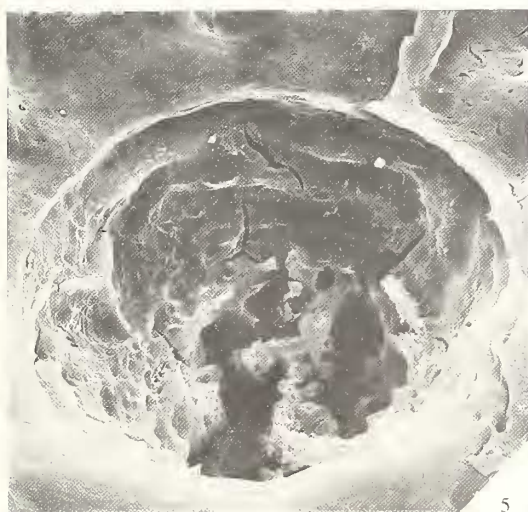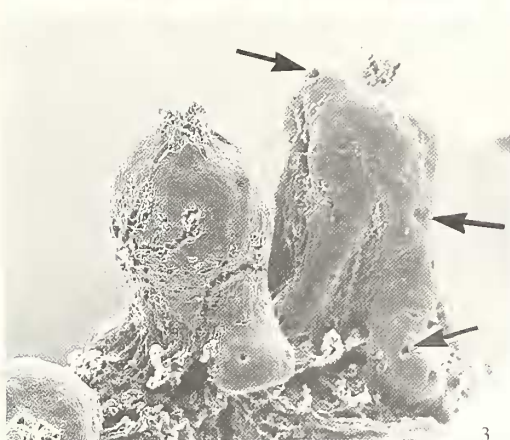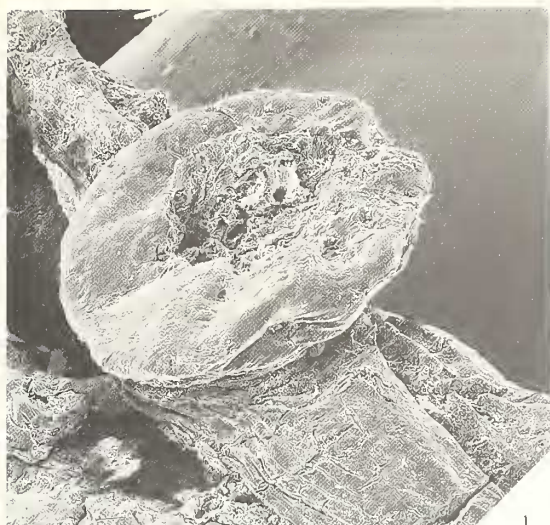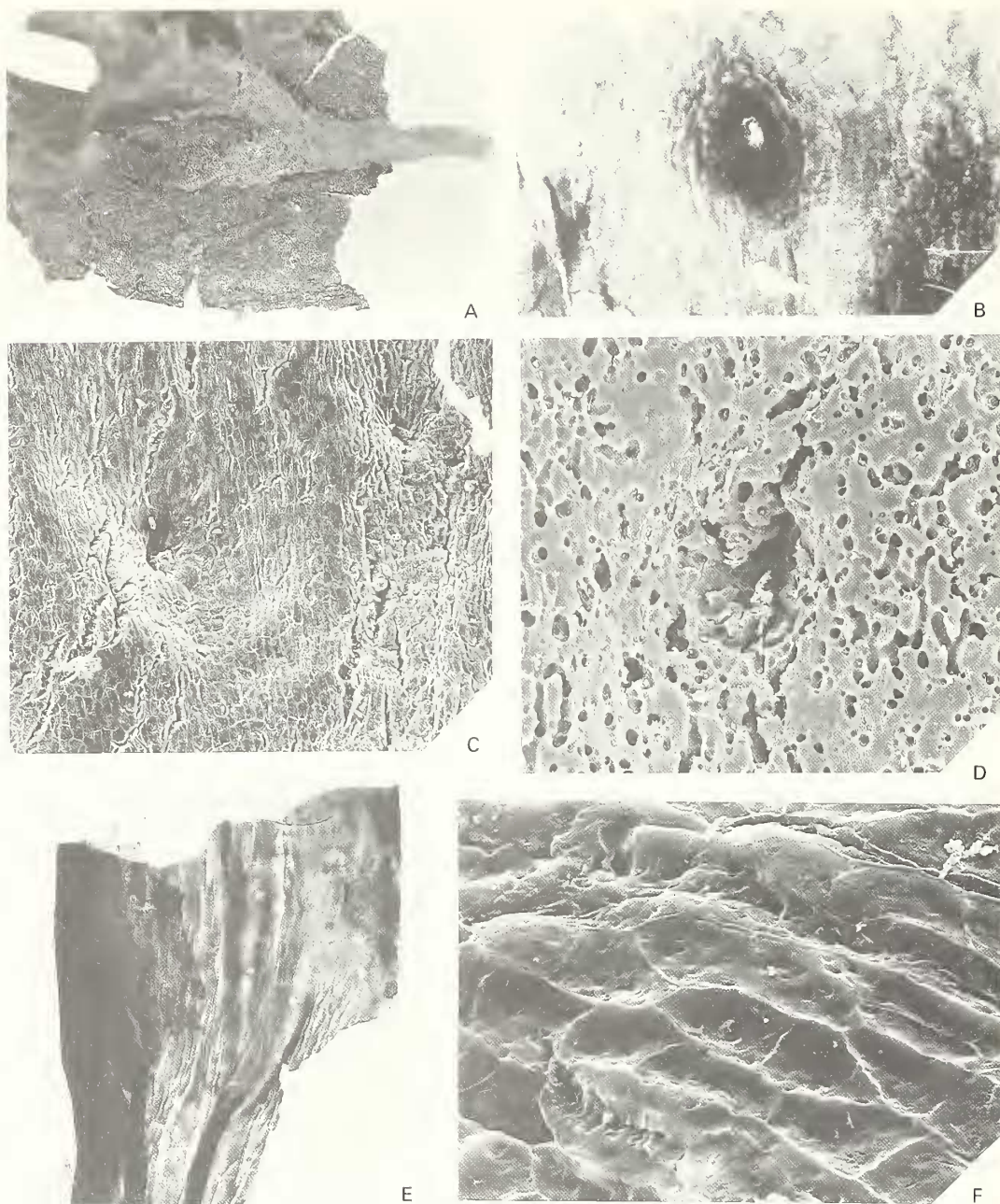
TEXT-FIG. 5. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. A, interior contents of a thallus, GSC 93014, × 14. B, LM of pore on thallus cleared with Schulze's solution until nearly translucent; region around pore is darker than rest, GSC 93020, × 65. C, SEM of inner cuticle surface, poral side, showing outlines of rectangular cells; pore in centre, × 110. D, SEM of inner cuticle surface, poral surface, appearing vermiform, probably a result of degradation or borings; pore in centre, × 220. E, ventral surface of extensively cleared thallus with characteristic longitudinal folds, GSC 93018, × 31. F, SEM of inner cuticle surface showing rectangular cell outlines; this probably reflects type of cell construction immediately below the cuticle, × 550.

Thickness of the poral, presumed upper surface is 75–250 μm, and that of the aporal one is about 30–60 μm. However, the form 3 thalli exhibit poral and aporal surfaces of more equal thickness. The thinner lower thallus surface often is partly broken down or may be entirely absent (Text-fig. 5A). Intact lower surfaces have been observed mostly near the tips of some lobes and rarely on more completely preserved specimens. Where present, the lower surface exhibits longitudinal ridges and appears fragile and rather wrinkled except at the margins where it is transitional to the thicker, upper surface (Text-fig. 5E).

Inside the thallus occurs a thin granular layer of material which is usually light-brown in colour (Text-fig. 5A). We do not believe this is rock matrix (left after HF treatment) but is a remnant of the internal contents of the thalli.

SEM of a cut transverse section of the thallus cuticle end-on shows it to be amorphous (Pl. 3, fig. 3). Thin sections examined with LM and TEM show an absence of internal structure in the cuticle, except for minute structures perpendicular to the outer surface interpreted as borings or cracks (Pl. 3, figs 1, 2, 4). Particularly interesting is the absence on all but a few specimens of regular ridges or pegs corresponding to depressions between epidermal cells as usually occurs on vascular plant cuticles or in other species of *Spongiophyton*. However irregularities of the inner surface of the cuticle may represent the position of anticlinal walls in life (Pl. 3, fig. 1). Possibly many such ridges were lost or obscured through erosion of the inner cuticle surface.

Examination of the interior cuticle surface has revealed few with cellular patterns (Text-fig. 5C, F). More frequently they exhibit a vermiform pattern (Text-fig. 5D) which compares well with the 'borings' described by Chaloner *et al.* (1974) for *S. nanum* from Ghana. Cleared thalli may exhibit an apparent cell-like pattern (Pl. 3, figs 5 and 6), especially in photographs. Close examination suggests these result from cracks caused by differential breakdown of the cuticle after prolonged oxidation. We term this a **pseudocellular pattern** and regard it as different from the cell outlines preserved on some inner cuticle surfaces.

Elemental analysis of two different specimens show element ratios similar to the Ghana *Spongiophyton* specimens (Table 2).

TABLE 2. Elemental percentage composition of *Spongiophyton* from Canada and Ghana. The difference of the sum from 100 is probably accounted for by oxygen.

	N	C	H	S
S. minutissimum, Canada	1·18	74·88	8·08	0
S. minutissimum, Canada	1·03	69·01	7·55	0
S. nanum, Ghana	2·70	78·40	8·40	—

COMPARISONS AND DISCUSSION

The thalli are clearly referable to the genus *Spongiophyton* Kräusel as emended by Chaloner *et al.* (1974). Characters considered diagnostic of the genus by the latter authors, and exhibited by the Canadian material, are: a tubular thallus with cuticular covering, dichotomous or sub-dichotomous branching and rounded apices; cuticle with internal cellular reticulum and circular-fusiform pores largely confined to one surface of the thallus. The Canadian specimens are older and morphologically more diverse than other undoubted *Spongiophyton* specimens. The thalli branch much more frequently and in more than one plane, and also bear more short vertical branches than previously known. Our data also confirm the interpretation of Chaloner *et al.* (1974) that some features considered diagnostic by Kräusel (dark bodies on surface, the 'spongy' or hyphal pattern) are in fact the result of degradation, either during preservation or the clearing process, of the thick cuticles. A pseudocellular pattern may result from cuticular breakdown in the Canadian specimens. The constrictions common in the Canadian thalli probably are a result of preservational factors or may reflect environmental fluctuations.

Species of Spongiophyton

The Canadian specimens are most similar to Kräusel's species *S. minutissimum*, based on consideration of his few illustrations and brief description and on study of his figured specimens. Many extensively cleared thallus fragments from Canada are identical to *S. minutissimum* in

exhibiting thickened margins, a character considered by Kräusel as distinctive for that species. Thallus appearance, cuticle thickness, and pore shape, size, and density of the Canadian material corresponds very closely to *S. minutissimum*. Two possible differences exist – maximum thallus width in the type material (up to 5 mm) exceeds that of the Canadian fossils and the dark bodies described by Kräusel for *S. minutissimum* are not found on the Canadian specimens.

The more extensive preservation and greater abundance of specimens from Canada provides some characters not available from the type material, limiting further comparison. In the absence of major characters separating them, and indeed with strong evidence supporting their identity, it seems reasonable to expand the concept of a known species rather than create a new one.

Differences between the Canadian specimens and other species of *Spongiophyton* include pore morphology and size, thallus size, and cuticle thickness. *S. nanum* and *S. lenticulare* are the best known species. The Canadian specimens differ from *S. nanum* in their smaller pores that mostly lack a bevelled margin. Branching is more profuse in the Canadian specimens than in *S. nanum* where only a few dichotomies or vertical branches have been recorded. Thallus diameter is half that of *S. nanum*. Cuticle thickness of the Canadian specimens (up to 250 μm) is much greater than that of *S. nanum* (60–80 μm) and both exceed the thickness of most vascular plant cuticles.

Similarly, the Canadian specimens differ from *S. lenticulare* in pore morphology, those of the latter species being elongate, slit-like structures with folded edges of cuticle extending to the outside, and their thicker cuticle. The internal cellular pattern of *S. lenticulare* consists of more elongate cells than occur in either *S. nanum* or the Canadian material.

Kräusel and Venkatachala (1966) placed *S. hirsutum* in *Aculeophyton*, because of its hairlike papillae. Kräusel's species *S. articulatum* is based on broken cuticle fragments which exhibit a very pronounced longitudinal striped pattern and transverse corrugations. These remains bear some resemblance to very over-macerated thalli from Canada, but are too poorly known for further comparison.

Notably absent in all of these species is any evidence of reproductive structures. Chaloner *et al.* (1974) suggested that the short vertical branches present on *S. nanum* thalli were perhaps sites of reproductive organs, but no conclusive evidence was obtained. Many short vertical branches of the Canadian specimens which exhibited depressions were examined for evidence of spores or other possible reproductive structures. Occasionally a mesh-work of material was present in the depressions, but more commonly only fissures were observed along the margins. Both types of structure are interpreted to have resulted from degradation of cuticle in apical regions.

Other identifications of thalli as *Spongiophyton* are less certain. Boureau and Pons (1973) assigned thalli from Bolivia to *S. lenticulare*. Pore shape agrees with that of Kräusel's *S. lenticulare* but some other features are problematical, recalling protuberances termed 'capsules' (see below) in *Orestovia* and other genera by Istchenko and Istchenko (1981). The Canadian specimens differ, not only in pore outline, but also in lacking dark round bodies and any evidence of internal 'hyphal ramifications' as described for the Bolivian specimens. The latter should be compared more closely

Figs 1–7. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. 1, ground thin section of thallus in rock matrix, showing much thicker poral and thinner aporal surfaces; dark contents in middle may be remains of inner cells and may correspond to the lighter material seen in Text-fig. 5A, × 54. 2, TEM of cuticle showing absence of internal structure, except for possible borings, × 700. 3, SEM of transverse cut surface end-on showing differential thickness of poral and aporal surfaces and absence of structure other than borings, × 280. 4, LM of section of cuticle showing borings, × 300. 5–7, cleared thalli showing breakdown of cuticle producing a pseudocellular pattern; 5, cleared thallus fragment with thicker margins as illustrated by Kräusel as typical of this species; some evidence of pseudocellular pattern at arrow, shown enlarged in fig. 6, GSC 93019, × 31; 6, detail of pseudocellular pattern of specimen in fig. 5, can be emphasized by manipulating lighting of microscope; several pores visible, apparently 'ringed' by pseudocellular pattern, GSC 93019, × 65. 7, over-cleared cuticle with spongy appearance similar to several illustrated by Kräusel, × 39.

PLATE 3

GENSEL, CHALONER and FORBES, *Spongiophyton*
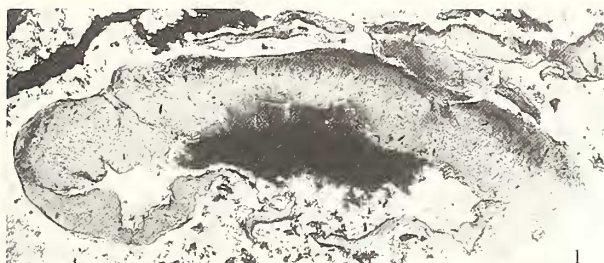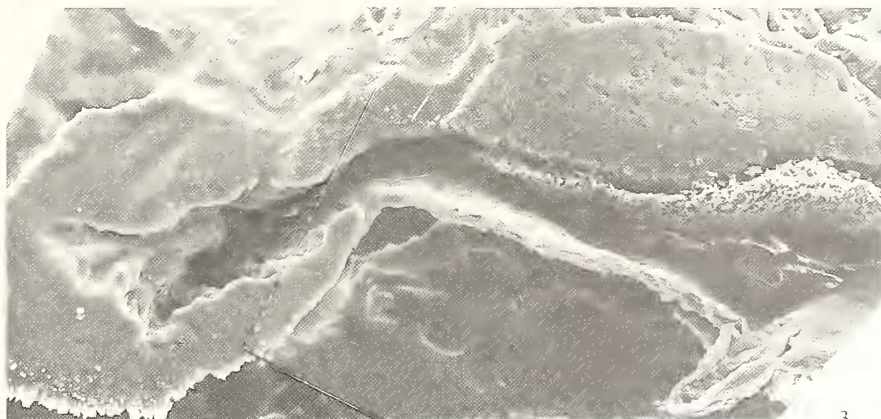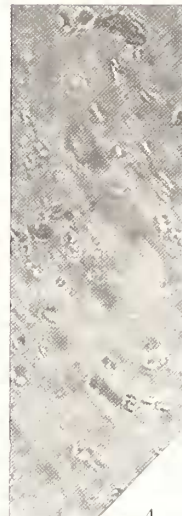
to the several thalloid types described by Istchenko and Istchenko (1981) from the Voronezh anticline, USSR.

As noted earlier, the specimens described as *Spongiophyton* by Zdebska (1978) may in fact represent other taxa. Although Zdebska's species 1 bears a superficial resemblance to *Spongiophyton* thalli, no details of pore type or cellular construction are evident. Species 2 consists of fragmentary cuticles with isodiametric cell outlines and pores, suggesting a filamentous rather than parenchymatous organization. Neither type shows any indication of being part of a tubular thallus like *Spongiophyton*. Edwards (1982) suggested that these fragments resemble some cuticles of *Nematothallus*.

Other putative spongiophytes

Other genera are allied with *Spongiophyton* in the family Spongiophytaceae (Table 1) because they exhibit a thalloid construction with thick, resistant, sometimes flexible cuticles and lack definitive evidence of reproductive structures. Comparison of these taxa is hampered somewhat because interpretation of particular morphological structures varies, depending on the worker involved or the time of publication and corresponding knowledge of Devonian plant diversity. It also is extremely difficult to interpret structural detail on opaque cuticles of comparatively undifferentiated organisms from photographs and descriptions. The cuticles of these other taxa may also have been strongly affected by taphonomic factors and preparation techniques. Thus the family may not be as coherent as it appears.

The broad, ribbon-like cuticularized axes of *Orestovia* are generally similar to *Spongiophyton* but longer, wider, less frequently branched, radially symmetrical, and with a thinner cuticle. The outer surface is smooth or covered with some form of tiny emergence (depending on author). Circular pores with slightly raised margins, often bordered by several concentric layers of mostly isodiametric 'cells', occur randomly. Extraporal regions bear the outline of elongate-rectangular cells. The pores and associated structures are interpreted by some workers as stomata (Ergolskaya 1934, 1936; Krassilov 1981), and by others as reproductive structures (Kräusel and Venkatachala 1966, Istchenko and Istchenko 1981). Krassilov (1981) further reported the presence of conducting cells with thickened wall patterns in *Orestovia*, suggesting it may be a vascular plant. Our preparations of thalli, conforming to Ergolskaya's *O. petzii* from the Barzas coal, support some of his conclusions concerning stomata. Krassilov's specimen appears papillate (= *O. devonica* of Ergolskaya), whereas the specimens available to us are smooth. Obviously, further documentation is needed to resolve several attributes of the genus. Despite this, *Spongiophyton*, including the Canadian material, can be distinguished from *Orestovia* in gross thallus organization, symmetry, and details of pore construction.

The genus *Aculeophyton* was established by Kräusel and Venkatachala (1966) for cuticular fragments of thalli from western Siberia, originally placed by Ergolskaya (1934, 1936) in *Orestovia devonica*. The genus differs from *Orestovia* mainly in the presence of papillae, conical in *A. sibirica* and hair-like in *A. hirsutum*. Krassilov considered that other characters outweighed the presence of papillae and that *Aculeophyton* and *Orestovia* are synonymous.

Istchenko and Istchenko (1981) described several new genera and species of thalloid plants from the Lower Devonian of the Voronezh region, USSR, placing some in the Spongiophytaceae and some in a second family, the Bitelariaceae. Bitelarian cuticles reflect distinct 'cell' patterns interpreted by the Istchenkos as a meristoderm (without a cuticle) and by Johnson and Gensel (1989) as a cuticular epithelium. A number of other characters such as branching pattern and presence of vascular tissue in *Bitelaria*, further distinguish bitelarians from all thalli placed in the Spongiophytaceae, as summarized in Johnson (1989) and Johnson and Gensel (1987, 1989).

Istchenko and Istchenko (1981) assigned the Voronezh fossils to several genera (*Orestovia*, *Orestovites*, *Voronejiphyton*, *Rhytidophyton*, *Bitelaria* and *Donotela*) relating them to the algae. They interpreted the protruding round pores found on thalli of the first four genera as reproductive structures (termed capsules) reminiscent of conceptacles or nemathecia, as found in brown and red algae. When mature, each structure supposedly opened and released its contents, leaving behind a pore. The same structures in *Orestovia* appear to us very like sunken stomata or in some cases like

the dark bodies or 'grossorgane' of Kräusel and Venkatachala (1966). No evidence of 'capsules' or stomata exists for the Canadian *Spongiophyton*.

Rhytidophyton superficially seems most similar to *Spongiophyton* but apparently consists of radially symmetrical tubular thalli with pronounced vertical folding. The thalli are up to 0·6 cm wide and dichotomize, with the resultant branches forming a U-shaped pattern. One or more hemispherical protuberances 1·5–3·5 mm in diameter occur just below the dichotomy, or singly elsewhere on the thallus, which when lost form large pores. Capsules (or the oval apertures that remain after their disintegration) are irregularly distributed on the thallus surface. The thallus is interpreted as consisting of an outer cuticle, a middle fibrous zone, and an inner region of coal. *Voronejiphyton* Istchenko and Istchenko (1981), based on a few specimens, is very similar to *Rhytidophyton*, apparently differing in exhibiting occasional longitudinal ridges and internal wall thickening. In addition to lacking 'capsules', *Spongiophyton* lacks obvious folds and exhibits a single-layered thick cuticle. Its short vertical branches usually are more extensively developed or larger than those of *Rhytidophyton* and are not located at points of branching.

Orestovites is similar to *Orestovia*, differing only in rather minor features, such as the presence of several cuticle layers, hemispherical structures, major cracks in the cuticle and an irregular pattern of cells on the inner cuticle surface.

## Other thalloid Devonian plants

Chaloner *et al.* (1974) compared *Spongiophyton* with several other Devonian plants of thalloid construction but with one or more features attributed to land plants, e.g. *Prototaxites*, *Parka*, *Protosalvinia* and *Nematothallus*. They all differ in apparently lacking the type of tubular cuticularized thallus plus pores seen in *Spongiophyton*, *Orestovia* and *Auculeophyton* and detailed comparison of most of them is unnecessary. It is intriguing to note, however, that the vertical branches of the Canadian *Spongiophyton* resemble the proposed reconstruction of *Protosalvinia* by Niklas and Phillips (1976) even though many differences between the two taxa exist, including their postulated mode of growth (Niklas and Chaloner 1976). Reproductive structures are known for *Protosalvinia*.

The several types of isolated cuticles attributed to *Nematothallus* (sensu Edwards 1982) or *Cosmochlaena* (Edwards 1986) have been compared at times with *Spongiophyton* or other spongiophytes. These latter plants differ from *Nematothallus*, as stated by Edwards (1982), in their tubular construction and apparently parenchymatous cell structure. Further, the isolated nematophyte cuticles are not as thick as those of *Spongiophyton* and some related taxa. The original concept of *Nematothallus* was of a system of tubes covered on the upper, and perhaps lower, surface by a cuticle and possibly bearing spores among the tubes. Edwards suggested the nearly isodiametric cell outlines of the associated cuticles represented outlines of filament tips. This taxon, and *Prototaxites*, served as the basis for Lang's Nematophytales (Lang 1937). While he suggested other taxa may be included in that group, later research has shown several of them to be differently constructed. We agree with Edwards (1982) that *Spongiophyton* probably had a parenchymatous organization, which would contrast strongly with the above taxa. We also believe the term nematophyte should be restricted to plants of tubular (filamentous) construction as originally proposed by Lang, thus excluding *Protosalvinia*, the Spongiophytaceae, and probably several other enigmatic early land plants (Strother 1988).

Proposed growth habit

The extensively preserved Canadian *Spongiophyton* provides a basis for modifying concepts of its growth habit. The dorsiventral, probably cross-sectionally elliptical, tubular nature of thallus lobes is confirmed. Profuse branching, both in the same plane and at right angles, produces a growth form recalling that of some thallose liverworts such as *Conocephalum* or *Marchantia*. This extensive branching is not consistent with or feasible to the growth model proposed by Niklas and Chaloner (1976) based on studies of *S. nanum*. Whether *S. minutissimum* actually grew differently from *S. nanum* is unclear; certainly data concerning multidimensional branching were sparse at the time the model was proposed.

These specimens are found in fluvial sediments, some appearing more extensively transported than others. Their habitat may have been similar to that of many extant thallose liverworts – stream or pond margins on a flood plain. They probably formed mats or stands several centimetres to tens of centimetres broad. The stacks of thalli found at the Athoville locality document that several levels of branches may occur on a single organism, as if the older portions were partially buried and newly produced ones grew upwards (towards light?). Where thalli have been sectioned *in situ* in the matrix, the thicker (presumably upper) surface is commonly uppermost in the rock, but not consistently enough to support the possibility of the plants growing within the environment of deposition. The short vertical branches appear different from other thallus lobes, but perhaps they elongated and became more parallel to the main thallus when older, as suggested by the specimen illustrated in Text-figures 2ᴇ and 4*k, n*. Variation in branching and thallus orientations are depicted in the reconstruction in Text-figure 6.
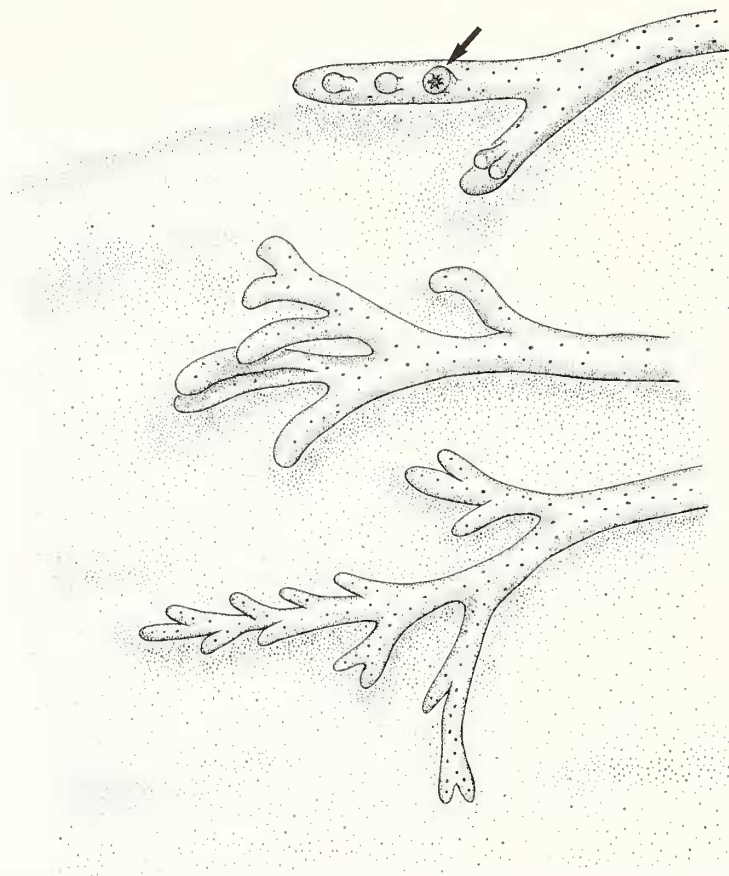
TEXT-FIG. 6. Proposed reconstruction of *Spongiophyton minutissumum* plants.

The question of affinities

Despite the abundance and variety of specimens of *S. minutissimum*, many questions remain particularly on the nature of its reproductive structures and whether or not it possessed conducting tissues. This has important bearing on its affinities – particularly in relation to whether it represents an 'algal' grade of organization or one more comparable with embryophytes. It appears to be a non-vascular plant with a resistant cuticle and pores.

A resistant cuticle is generally regarded as an adaptation to a terrestrial habitat, since only terrestrial higher plants (= embryophytes) are known to possess one. Mishler and Churchill (1984,

1985) and others have postulated that a cutin-containing cuticle is a synapomorphy of the embryophyte clade. This might be further tested by chemical analysis of the cuticles of several plant types, including representatives of the charophyte-embryophyte clade, representatives of other algal clades that possess an outer covering, and of the enigmatic types discussed above. If lipid-rich (cutin-containing) cuticles occur only in the embryophytes, and if *Spongiophyton* cuticles have a similar composition, then one could place it in that lineage. The same might be true of *Orestovia* or other taxa of enigmatic affinity.

Thus, although the thalloid, presumed parenchymatous construction of *Spongiophyton* has led workers to suggest it is related to algae, one could also envision it representing an algal-derived form that had not yet attained the grade of complexity of bryophytes or vascular plants. Its affinity to the charophyte-embryophyte clade *sensu* Mishler and Churchill (1984, 1985) remains uncertain as it is possible that several extinct lineages, derived from any of several algal clades, may have become adapted for terrestrial existence and possessed a resistant cuticle. More fossils of these enigmatic types, and careful analysis of all aspects of morphology and chemistry, might address these questions. Documenting all combinations of adaptations to a terrestrial existence among Silurian-Devonian plants promises to reveal more fully the intricate story of invasion of the land by plants and of diversity of lineages at that time.

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